

## SPECIFIC LEAF WEIGHT (SLW) AS RELATED TO THE YIELD AND ITS COMPONENTS IN RICE

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### Abstract

Specific leaf weight (SLW, mg/cm<sup>2</sup>) of 32 rice varieties was measured weekly during the two crop seasons at Nankang experimental farm in order to determine its feasibility as a selection indicator for grain yield in rice.

Changes in all traits measured (SLW, yield and its components) were different between the two crop seasons. Phenotypic correlations between SLW and the yield and its components were small in both crops. Yield of the first crop was much more closely related with panicle number. But it was highly associated with fertility rate and 1000-grain weight in the second crop. In the first crop, genotypic correlations between SLW and panicle number were negative and significant from the maximal tillering stage afterwards. However, panicle number as a result of the tiller development dominated over the relationship. In the second crop, SLW and yield was negatively correlated at the maximal tillering stage and also in one week before heading genotypically. However, panicle number was found to be associated with the SLW and yield relationship in the later growth. And above all, higher estimates of heritability for SLW were found only in the later growth stages in both crops. Thus, the improvement of rice yield through the selection of SLW is generally not practicable.

### Introduction

Dry matter production is of great importance to rice as it combines with the harvest index to determine grain yield (Yoshida, 1972). Shieh (1978) found that rice yield in both crops was positively correlated with dry matter accumulation of the rice plant during the period from panicle initiation to heading. Theoretically, an increase in the photosynthetic rate would increase crop yield, since photosynthesis is highly responsible for the dry matter production. Thus, increasing the photosynthetic rate through breeding appears to be a promising method for improving yield.

Specific leaf weight (SLW, dry weight per unit leaf area) could be taken as a selection trait for high yield of rice, because it is easily measured. Researches on the relationship between SLW and photosynthesis were undertaken in alfalfa, soybean, and reed canarygrass (Pearce *et al.*, 1969; Dornhoff & Shibles, 1970; Anake *et al.* 1977) and SLW was highly correlated with photosynthesis in each species. Kumura (1975) also used

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specific leaf area (SLA) which is the reciprocal of SLW as one of the parameters in expressing the relative growth of leaf area in rice. This led to a suggestion that SLW could be related to the relative efficiency of photosynthesis in rice. However, there have been no reports in the literature on the feasibility of selection for SLW in yield improvement of rice.

This experiment was therefore conducted to study the SLW of rice leaves in various weeks of growth in different crop seasons relating to their heritabilities, genotypic and phenotypic correlations. The role of SLW in the improvement of rice yield was evaluated for each growing season. Changes in yield and its components in each specific crop season were also investigated.

### Materials and Methods

Thirty-two rice varieties were used as the material in this study. Among them 16 were indica rice and 16 were japonica rice. They were set out in one block with 150 plants in 6 rows for each variety at Nankang experimental farm. The plants were arranged in rows with 25 cm between rows and 20 cm within the row. The date of transplanting was March 30, 1978 for the first crop and Aug. 20, 1978 for the second crop.

SLW measurements started from the third week in the first crop and from the second week in the second crop after transplanting. They were made weekly and terminated until the second week after heading. Five samples were taken from each variety at random. Leaves selected were the uppermost unfolded ones. The leaf area was determined by an automatic leaf area meter (Model Li-3000, LAMBDA Instruments Co.) in  $\text{cm}^2$  with an accuracy of  $\pm 1\%$ . The samples were dried at  $60^\circ\text{C}$  in an air-forced oven for 48 hours and their dry weight recorded. SLW was calculated as the ratio of the dry weight of leaves to the leaf area ( $\text{mg}/\text{cm}^2$ ).

A record of the yield and its components (i.e., panicle number, spikelet number per panicle, fertility rate, and 1000-grain weight) was kept for each variety after harvest. The statistical analysis of data was computed for each trait by taking the 32 varieties as one population. The analysis was directed to calculate the heritability of each trait, and the genotypic and phenotypic correlations among determinations of SLW, yield, panicle number, spikelet number per panicle, fertility rate, and 1000 grain weight according to the procedures suggested by Kempthorne (1957). Genotypic correlations among traits were furthermore subjected to estimate their similarity by the principal component analysis following Seal's (1972) suggestion.

### Results

Changes in specific leaf weight of rice leaves during the growing season between the first and the second crop were different (Fig. 1). SLW in the first crop increased rapidly as growth proceeded, whereas the changes for the second crop were mild.

Higher SLW's were found in the second crop during the early growth stages (SLW 1-6) than they were in the first crop, however, the averages persisted from SLW 7 there-

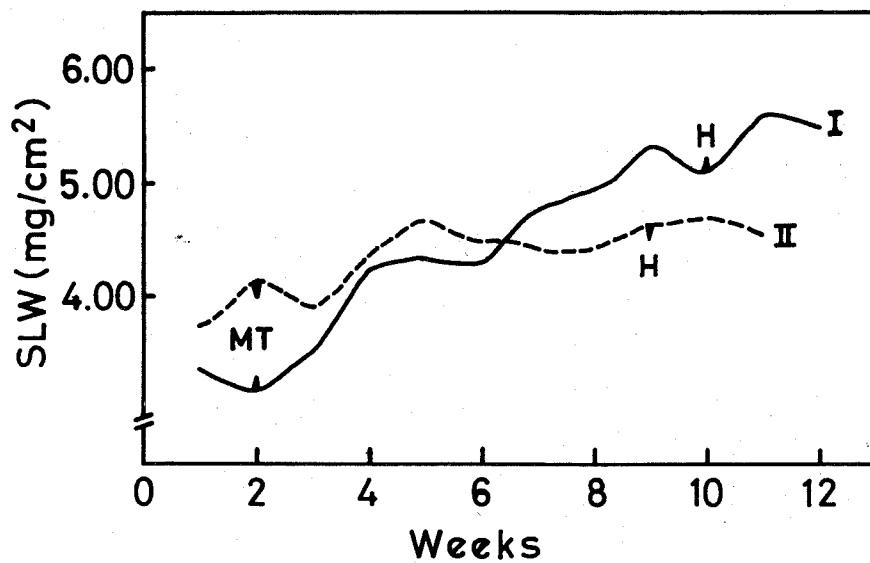


Fig. 1. Average SLW of rice leaves measured in different weeks for the first and the second crops.  
 MT represents the maximal tillering stage.  
 H represents the heading stage.

Table 1. Genotypic and phenotypic correlations among specific leaf weight measurements and heritabilities in twelve different weeks of the first crop

SLW	1	2	3	4	5	6	7	8	9	10	11	12
1.	.42	.65	.51	.81	.61	.63	.71	.64	.39	.68	.33	.26
2	.19	.27	.65	.59	.89	.47	.56	.44	.24	.61	.43	.46
3	.23	.21	.40	.83	.81	.73	.84	.57	.54	.57	.51	.35
4	.40*	.20	.40*	.45	.84	.78	.82	.84	.78	.61	.53	.38
5	.31	.38*	.39*	.43*	.55	.79	.90	.70	.63	.76	.69	.54
6	.29	.13	.26	.41*	.44*	.50	.92	.77	.62	.53	.38	.34
7.	.43*	.19	.42*	.51**	.54**	.54**	.58	.82	.68	.57	.43	.32
8	.26	.24	.21	.38*	.40*	.42*	.44*	.57	.75	.49	.52	.54
9	.20	.08	.27	.38*	.41*	.40*	.37*	.46**	.64	.85	.90	.77
10	.19	.27	.17	.24	.37*	.24	.31	.27	.33	.33	.98	.94
11	.14	.13	.25	.39*	.30	.23	.27	.27	.50**	.45*	.61	.94
12	.17	.14	.26	.22	.30	.22	.23	.38*	.52**	.41*	.59**	.68

\*and\*\*: Significant at the 0.05 and 0.01 probability levels, respectively. Estimates representing heritability of each week are shown along the diagonal, genotypic correlations are in the triangle above and phenotypic correlations in the triangle below. The maximal tillering stage occurred in this crop in the week of SLW 2 and the heading period was in SLW 10.

Table 2. *Genotypic and phenotypic correlations among specific leaf weight measurements and heritabilities in eleven different weeks of the second crop.*

SLW	1	2	3	4	5	6	7	8	9	10	11
1	.28	.83	.89	.68	.68	.65	.80	.29	.10	.41	.21
2	.16	.21	.78	.94	.64	.77	.79	.81	.69	.84	.60
3	.41*	.26	.41	.98	1.03	.86	.76	.61	.58	.66	.30
4	.18	.21	.31	.39	.88	.88	.72	.70	.78	.88	.62
5	.22	.28	.37*	.28	.31	1.01	.71	.52	.78	.60	.33
6	.26	.29	.41*	.35	.40*	.46	.72	.48	.64	.67	.36
7	.06	.19	.39*	.30	.17	.28	.30	.64	.56	.62	.25
8	.17	.31	.34	.25	.28	.28	.28	.55	.82	.74	.62
9	.06	.18	.26	.30	.21	.31	.22	.42*	.49	.81	.31
10	.21	.34	.33	.45*	.32	.32	.30	.42*	.47*	.64	.46
11	.06	.30	.22	.31	.16	.22	.11	.45*	.20	.36	.84

\*: Significant at the 0.05 probability level. Estimates representing heritability of each week are shown along the diagonal, genotypic correlations are in the triangle above and phenotypic correlation in the triangle below. The maximal tillering stage occurred in this crop in the week of SLW 2 and the heading period was in SLW 9.

after in the second crop and were exceeded by those in the first crop.

Genetic and phenotypic correlations within SLW's at various growing dates were positive in both crops (Table 1 & 2). Most of the correlations of any two neighboring dates had higher values than those obtained for any other two dates and suggested that the development of SLW during rice growth was not conducted singly by one gene pair. Heritability of SLW increased gradually with time in the first crop (Table 1) except for those at the maximal tillering stage (SLW 2) and during heading (SLW 10) indicating that the extent of environmental influence on SLW during the growth was in a decreasing manner. Significant phenotypic correlations were found also between SLW's that were nearer to each other by the week from the maximal tillering stage afterwards. And it seemed that after that particular stage the closer the dates of growth the more similar the environments that affected the performance of SLW. Therefore, selection for SLW of desiring trait for the first crop can be effective in the period after the 7th week of growth (SLW 5).

In the second crop, trends in relation to heritability of SLW on all dates of determinations were inconsistent except in the later portion of rice growth (SLW 8-11, Table 2). Higher heritabilities (.49 - .84) and significant phenotypic correlations in this period indicated that selection for SLW was executable only in the later growth stages for the second crop.

SLW served only poorly as a predictive character for rice yield, since SLW's over all dates in both crops were found to be phenotypically little or none correlated with yield and its components (Table 3 and 4). On the other hand, they showed more close genotypic relations with some of the yield components. Higher estimates were obtained with panicle

Table 3. Correlations between SLW in twelve different weeks and panicle number (PN), spikelet number per panicle (SN), fertility rate (FR), 1000-grain weight (GW), and yield (Y) in the first crop

	SLW 1		2		3		4		5		6	
	G	P	G	P	G	P	G	P	G	P	G	P
PN	-.27	-.06	-.19	-.05	-.37	-.14	-.60	-.31	-.55	-.29	-.39	-.17
SN	.09	.07	.11	.05	.47	.04	.25	.05	.22	.00	.22	.09
FR	-.13	.04	.37	.14	.20	.12	.35	.14	.49	.30	.39	.25
GW	.01	-.04	-.27	.09	.22	.11	.09	.00	.02	.02	-.15	-.11
Y	.02	-.03	.14	.05	.08	-.01	-.12	-.11	-.13	-.13	.07	-.01

	7		8		9		10		11		12	
	G	P	G	P	G	P	G	P	G	P	G	P
PN	-.38	-.23	-.35	-.11	-.55	-.24	-.41	-.22	-.52	-.14	-.36	-.17
SN	.12	.02	.16	.06	.10	.07	.37	.07	.34	.09	.20	.11
FR	.53	.31	.59	.35	.42	.28	.17	.02	.16	.09	.15	.12
GW	-.06	-.04	-.31	-.17	-.14	-.06	-.06	-.00	-.06	-.06	-.22	-.16
Y	-.05	-.08	.13	.07	-.24	-.08	-.13	-.12	-.28	-.08	-.26	-.08

G denotes the genotypic correlation and P denotes the phenotypic correlation.

number and fertility rate in the first crop (Table 3). They were  $-.37$ — $.60$  for the former starting from SLW 3 thereafter and  $.42$ — $.59$  for the latter in the period of pre-heading storage (SLW 5-9).

In the second crop, yield was high in its relation with SLW at the maximal tillering stage (SLW 2,  $\gamma_g = -.73$ ) and in one week before heading (SLW 8,  $\gamma_g = -.45$ ). Fertility rate and 1000-grain weight were also strongly associated with SLW at the maximal tillering stage genotypically as the correlations showed  $-.64$  and  $-.65$  for fertility rate and 1000-grain weight, respectively.

Yield of the first crop was highly associated with the number of panicle ( $\gamma_g = .63$ ;  $\gamma_p = .70$ , Table 5), however, low heritability of the component (0.30) indicated a higher degree of influence from the environments. Spikelet number per panicle was the next component that affected yield in the first crop ( $\gamma_p = .37$ ), still, it responded to the environmental changes ( $\gamma_g = .13$ ). Fertility rate and 1000-grain weight were the least affected by the environments according to their high heritabilities, nevertheless, they did not contribute much to yield. In contrast to that in the first crop, yield of the second crop was determined largely by fertility rate and 1000-grain weight (Table 6). Correlations of the two components with yield were relatively high phenotypically and genotypically, (yield/fertility rate:  $\gamma_p = .82$ ,  $\gamma_g = .89$ ; yield/1000-grain weight:  $\gamma_p = 0.53$ ,  $\gamma_g = .70$ ), heritability being 0.79 for fertility rate, 0.61 for 1000-grain weight, and 0.64 for yield was high and significant.

**Table 4.** Correlations between SLW in eleven different weeks and panicle number (PN), spikelet number per anicle (SN), fertility rate (FR), 1000-grain weight (GW), and yield (Y) in the second crop

	SLW 1		2		3		4		5		6	
	G	P	G	P	G	P	G	P	G	P	G	P
PN	-.16	-.00	.30	-.04	-.52	-.25	-.34	-.21	-.24	-.08	-.29	-.13
SN	.35	.16	.39	.14	.70	.37	.55	.30	.63	.22	.41	.21
FR	-.26	-.10	-.64	-.29	-.27	-.17	-.28	-.14	-.35	-.23	-.23	-.12
GW	-.45	-.15	-.65	-.25	-.40	-.23	-.44	-.16	-.34	-.06	-.35	-.21
Y	-.25	-.03	-.73	-.24	-.28	-.14	-.25	-.16	-.27	-.06	-.15	-.07

	7		8		9		10		11	
	G	P	G	P	G	P	G	P	G	P
PN	-.23	-.09	-.40	-.21	-.41	-.11	-.41	-.24	-.25	-.15
SN	.47	.17	.23	.09	.32	.18	.49	.35	.26	.20
FR	-.33	-.12	-.28	-.17	-.18	-.17	-.30	-.19	-.15	-.12
GW	-.38	-.20	-.22	-.11	.09	.06	-.16	-.11	-.30	-.21
Y	-.25	-.07	-.45	-.24	-.20	-.13	-.33	-.19	-.25	-.18

G denotes the genotypic correlation and P denotes the phenotypic correlation.

**Table 5.** Genotypic and phenotypic intercharacter correlations involving rice yield and its components in the first crop

	PN	SN	FR	GW	Y
PN	.30	.39	-.27	-.04	.63
SN	.05	-.28	-.55	-.01	.13
FR	-.09	-.27	-.58	-.16	-.05
GW	-.11	-.12	.05	.69	.17
Y	.70**	.37*	.18	.03	-.18

\*and\*\*: Significant at the 0.05 and 0.01 probability levels, respectively. Estimates representing heritability of each character are shown along the diagonal, genotypic correlations are in the triangle above and phenotypic correlations in the triangle below.

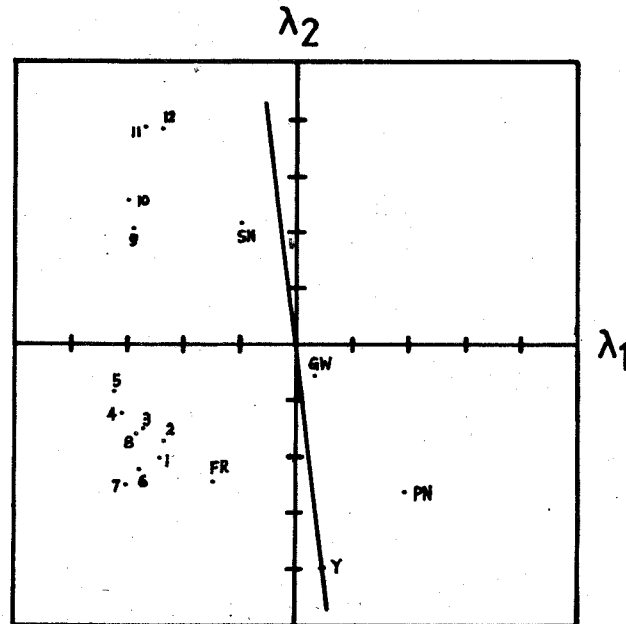


Fig. 2 Scatter diagram over all genotypic estimates for the first crop season through the principal component analysis plotted by the vectors with  $\lambda_1$  against  $\lambda_2$ . The numerical symbols indicate the SLW measurements in 12 different weeks. PN stands for panicle number, SN for spikelet number per panicle, FR for fertility rate, GW for 1000-grain weight, and Y for yield. The accumulated percentage for  $\lambda_1$  and  $\lambda_2$  is 63.57.

Table 6. Genotypic and phenotypic intercharacter correlations involving rice yield and its components in the second crop.

	PN	SN	FR	GW	Y
PN	.61	-.59	-.13	.13	.13
SN	-.46**	.66	-.37	-.20	-.31
FR	-.11	-.28	.79	.54	.89
GW	.03	-.05	.44*	.61	.70
Y	.23	-.15	-.82**	.53	.64

\*and\*\*: Significant at the 0.05 and 0.01 probability levels, respectively. Estimates representing heritability of each character are shown along the diagonal, genotypic correlations are in the triangle above and phenotypic correlations in the triangle below.

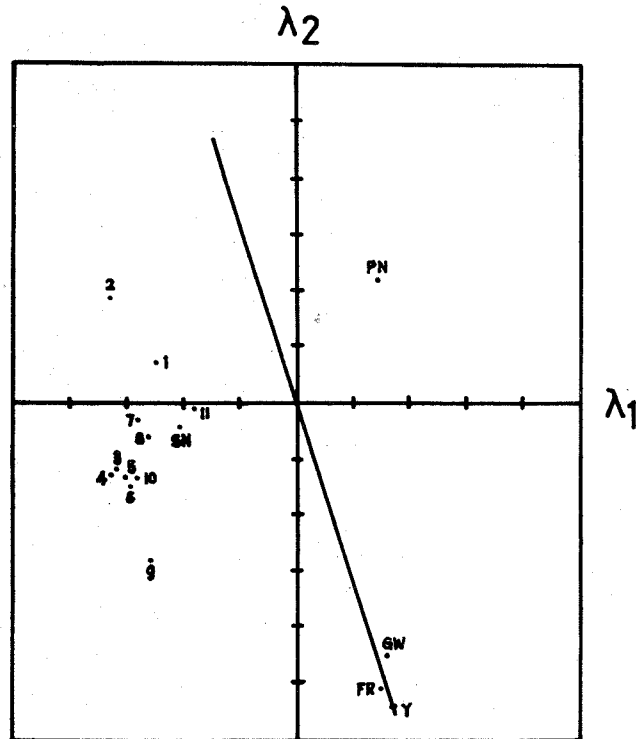


Fig. 3. Scatter diagram over all genotypic estimates for the second crop season through the principal component analysis plotted by the vectors with  $\lambda_1$  against  $\lambda_2$ . The numerical symbols indicate the SLW measurements in 11 different weeks. PN stands for panicle number, SN for spikelet number per panicle, FR for fertility rate, GW for 1000-grain weight, and Y for yield. The accumulated percentage for  $\lambda_1$  and  $\lambda_2$  is 68.83.

Results based on the principal component analysis of all genetic correlations are shown in Fig. 2 and Fig. 3. They revealed much the same facts as the results by single correlation method has shown. Except that in the first crop (Fig. 2), SLW over 12 dates of determination could clearly be divided into 2 groups, namely vegetative stage (SLW 1-8) and reproductive stage (SLW 9-12). SLW's in the vegetative stage were closely related with fertility rate implying that the fertility rate depended more on the preheading assimilates storage. On the other hand, spikelet number per panicle was found to be slightly linked to SLW's in the reproductive stage, but it was in fact caused by the negative effect of the panicle number.

Different groups of SLW's were also found in the second crop (Fig. 3). Changes in SLW were split at the maximal tillering stage. Yield was highly correlated with fertility rate and 1000-grain weight. However, SLW's from the maximal tillering stage thereafter were all not related with yield.

#### Discussion

As measured in this experiment, SLW was a poor indicator of selection for high rice yield in both crop seasons. Changes in SLW of rice leaves were found to be highly envi-



ronmentally controlled. Kumura (1975) reported that temperature and solar radiation worked upon SLW in an opposite direction. Temperature affected SLW negatively and solar radiation affected SLW positively almost in all cases.

Changes in SLW are different between the two crops. SLW tends to increase with the advancement of growth. Its increment is greater for the first crop than for the second crop. High initial SLW averages were found in the second crop, however, they persisted and were eventually exceeded by those in the first crop in the middle of growth. The greater increase in SLW of rice leaves in the period of preheading storage and during heading of the first crop season indicates more dry matter is produced at those particular times. And this is important for grain filling which in turn increases grain production.

SLW is also genetically associated with tiller number (or panicle number) in the physiological sense. Its negative association appears to be stronger after the completion of tillering. The effect reaches the highest level during heading in both crops suggesting that, by genetic nature, the vegetative growth and grain filling are interrelated to each other and in combination to determine yield.

Changes within SLW's during the entire growth may not be of the single gene pair effect, however, stronger genetic influence exists during a certain period of each crop (after the maximal tillering in the first crop and during the grain filling stage in the second crop.) Nevertheless, yield potential of rice can not easily be estimated simply by the SLW evaluation, as SLW was poorly correlated with yield and its components phenotypically.

Panicle number is the largest factor that changes the yield performance in the first crop season. After the maximal tillering stage, it is genetically negatively linked to SLW. This relationship comes rather as a consequence of the tiller number development. It is the tiller number that changes SLW. More tillers results in more number of panicle and smaller SLW in later period of growth. This phenomenon can be found also in the second crop, however, low temperature in early vegetative growth is particularly detrimental in the first crop as it seriously reduces tiller number. Since tiller number cannot be altered through any genetic manipulation of SLW, effective measures have to lie on suitable cultivation methods to minimise the climatic effects, e.g., by adjusting planting dates, controlling the depth of water in the paddies.

In the second crop, fertility rate and 1000-grain weight in turn limit rice yield. Of particular interest is that fertility rate was negatively associated with SLW over all dates of measurement in the second crop, whereas a positive correlation between the two was found in the first crop (especially during the period of the pre-heading storage). From this observation, it seems that thin leaf varieties are expedient under the climate of the second crop in which solar radiation is declining during the grain filling stage, on the other hand, thick-leaf varieties are preferred in the first crop as its solar radiation is not limited. 1000-grain weight can also be gained in thin-leaf varieties in the second crop, but other climatic factors may somehow be influential. Temperature, as Tsunoda (1975) pointed out, was the important factor affecting the translocation of assimilates in the rice plants. This accounts for the reason why 1000-grain weight of the second crop fluctuates more readily in different years with different records of temperature (Luo *et al.*, 1979). Accordi-

ing to Murata & Matsushima (1969), it was an adaptation of rice to develop thin, large leaves under weak light condition. The physiological significance behind such an adaptation was furthermore indicated by Tsunoda (1977). His evidences showed that thick leaves were superior to thin leaves in their photosynthetic rate under high solar intensity, but there was only little difference in photosynthesis with leaves of different thickness under weak light condition. However, under low light intensity, the rate of respiration was higher for thick leaves than for thin leaves. Therefore, he concluded that thick-leaf varieties were better in high solar intensity and thin-leaf varieties in low solar intensity.

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#### Literature cited

- Anake T.N., I.T. Carlson and R.B. Pearce 1977. Direct and correlated responses to selection for specific leaf weight in reed canarygrass. *Crop Sci.* 17:765-769.
- Dornhoff G.M. and R.M. Shibles 1970. Varietal difference in net photosynthesis of soybean leaves. *Crop Sci.* 10:42-45.
- Kempthorne O. 1957. An introduction to genetic statistics. John Wiley & Sons Inc. N.Y.
- Kumura A. 1975. Leaf area development and climate. pp. 60-66. *In* Y. Murata (ed.) JIBP Synthesis, Volume 11, Chap. 2.4. University of Tokyo Press, Tokyo.
- Luo C.C., H.P. Wu and S.S. Yao 1979. Fundamental researches for higher yield of rice in Taiwan (II), (I) Studies on the differences of rice ripened rate between 2 crop seasons under various growth conditions. *National Science Council Monthly, R.O.C.* 7(7):692-699. (in Chinese with English summary).
- Murata Y. and S. Matsushima 1969. Rice. pp. 73-99. *In* T. Evans (ed.) *Crop Physiology*, Chap. 4. Cambridge University Press
- Pearce R.B., G.E. Carlson, D.K. Barnes, R.H. Hart, and C.H. Hanson 1969. Specific leaf weight and photosynthesis in alfalfa. *Crop Sci.* 9:423-426.
- Shieh Y.J. 1978. Dry matter production in rice community. pp. 29-38. *In* W.C. Chang and Y.J. Shieh (eds.) *Photosynthesis and Plant Productivity*, Monograph No. 2 of Inst. of Botany, Academia Sinica, Taipei, Taiwan, R.O.C. (in Chinese)
- Seal H.L. 1972. *Multivariate statistical analysis for biologists.* John Wiley & Sons Inc. N.Y.
- Tsunoda S. and K. Yamaguchi 1975. Regression of grain yield on leaf area index of rice pp. 145-149. *In* Y. Murata (ed.) JIBP Synthesis, Volume 11. University of Tokyo Press, Tokyo.

- Tsunoda S. 1977. Characteristic of photosynthesis and environmental adaptation of rice. *Heredity (Japan)* 31 (7):53-58. (in Japanese)
- Yoshida S. 1972. Physiological aspects of grain yield. *Ann. Rev. Plant Physiol.* 23:437-464.

## 水稻單位葉面積重量比 (SLW) 之變化與 稻作產量及其構成因素間之關係

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在南港地區種植 32 種水稻 (秈, 粳 各半), 分別於兩期作每週測取各品種之單位葉面積重量比 (SLW, mg/cm), 並於收穫時收集產量及其構成因素的資料, 再經由統計分析以觀察 SLW 是否適合作為產量育種選拔上之目標性狀。

本研究的結果顯示 SLW, 產量及其構成因素是隨期作之不同而異, 觀察產量及其構成因素與 SLW 間之表現型相關, 無論在一或二期作時皆很小。其影響產量者, 在一期作時主為穗數的多寡, 而二期作時則為稔實率及千粒重。

一期作時雖穗數與 SLW 間之遺傳型相關呈負值且在分蘗盛期後較為顯着, 然兩者間之關係實受稻株分蘗情形之影響, 即水稻分蘗的表現是致使穗數與 SLW 變化的主因。

二期作時 SLW 與產量間於分蘗盛期及抽穗前一週時, 皆呈負遺傳型相關。不過由於 SLW 之遺傳率在兩期作時只在生育後期出現較大值, 而 SLW 雖在抽穗前一週能影響產量, 但其原因主要是受穗數影響。故由以上分析可知, 欲經由 SLW 的選拔以提高本省稻作產量似乎不甚有效。